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DESCRIPTIONS OF TWO NOMEN NUDUM SPECIES OF *ANOLIS* LIZARD FROM NORTHWESTERN SOUTH AMERICA

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ABSTRACT. We describe two northern South American Pacific lowland species of *Anolis* that historically have been associated with names that are currently nomina nuda. *Anolis lyra* new species is similar to *Anolis vittigerus* but differs primarily in possessing smaller dorsal scales on the head and body and in color pattern. *Anolis anchicayae* new species is similar to *Anolis peraccae* and *Anolis fasciatus* but differs primarily in size and color pattern. We scored the new species for skeletal and external morphological phylogenetic characters and performed a parsimony analysis with 251 additional *Anolis* species using molecular and morphological data. *Anolis anchicayae* is sister to *A. peraccae* in a basal group of South American "alpha" *Anolis* ("dactyloids," "*latifrons*" group). *Anolis lyra* is placed with other *lemurinus*-group *Anolis* within the large clade of mainland "beta" *Anolis* ("*Norops*").

KEY WORDS: *Anolis anchicayae*; *Anolis lyra*; Colombia; Ecuador

RESUMEN. Describimos dos especies de *Anolis* de zonas bajas del Pacífico de Colombia y Ecuador que tradicionalmente han estado asociadas con nombres en *nomen nundum*. *Anolis lyra* sp. nov. es parecido a *Anolis vittigerus* pero se diferencia principalmente en que presenta las escamas del dorso de la cabeza y el cuerpo más pequeñas, y en el patrón de coloración. *Anolis anchicayae* sp. nov. es parecido a *Anolis peraccae* y *Anolis fasciatus* pero se diferencia principalmente en el tamaño y el patrón de coloración. Se codificaron caracteres filogenéticos de morfología externa y osteología y se realizó un análisis de parsimonia con 251 especies adicionales de *Anolis* usando una combinación de datos morfológicos y moleculares. *Anolis anchicayae* es taxón hermano de *A. peraccae* dentro de un grupo basal de especies suramericanas de *Anolis* "alfa." *Anolis lyra* esta relacionado con otras especies del grupo *lemurinus* dentro de un clado más grande compuesto por especies continentales de *Anolis* "beta."

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[4] Williams and Miyata are deceased and are included as coauthors for the following contributions. Poe was able to diagnose each species and identify MCZ specimens on the basis of Williams' unpublished notes, which clearly were influenced by Miyata's work on the second species described herein. Additionally, Williams is responsible for Figure 6. Subsequent to submission of this manuscript, the editor provided Poe with a chapter of Miyata's Ph.D. thesis, never published, describing the second of the two species described herein. Poe incorporated information from this manuscript into the diagnosis of this species.

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Ernest Williams and collaborators published a series of papers from 1983 to 1992 describing "new or problematic" *Anolis* from Colombia. These papers reviewed and expanded the Colombian anoline fauna and established the country as a center of diversity for the *Anolis* clade. The publication of these descriptions and other taxonomic works on Colombian lizards (e.g., Ayala and Castro, 1983) prompted the need for a summary of available information. Stephen Ayala (1986) obliged and produced a list of the 205 lizard species thought to occur in Colombia. This list included eight species of *Anolis* (and species in other clades) listed in quotes ("") and associated with authors to signal that descriptions were not yet published but were forthcoming. Published descriptions of *Anolis* species associated with four of these names soon followed (*A. danieli* Williams 1988, *A. ruizi* Rueda and Williams 1986, *A. lamari* Williams 1992, *A. medemi* Ayala and Williams 1988), but the other names have languished without descriptions as nomina nuda for over 20 years. The aim of this paper is to rectify this situation with respect to two of the remaining names well known to Colombian herpetologists.

MATERIALS AND METHODS

We consider species to be evolutionary lineages (Simpson, 1961; Wiley, 1978) and operationalize this concept by identifying species on the basis of consistent differences between populations. That is, we hypothesize that populations that are diagnosable by major differences in the frequencies of traits are distinct evolutionary lineages or species (see Wiens and Servedio, 2000).

Measurements were made with digital calipers on preserved specimens and are given in millimeters (mm), usually to the nearest 0.1 mm. Snout-vent length (SVL) was measured from the tip of the snout to the anterior of the cloaca. Head length was measured from the tip of the snout to the anterior edge of the ear. Femoral length was measured from the midline of the venter to the knee, with the limb bent at a 90-degree angle. Head width was measured at the broadest part of the head, between the posterolateral corners of the orbits. Comparisons were made with preserved material of the putative closest relatives of the new species, and with published species descriptions, preserved material, or both of more distant relatives (online Appendix 1). Scale terminology and characters used mainly follow standards established by Williams (e.g., Williams *et al.*, 1996) for species descriptions of anoline lizards. Skeletal description is given in terms of Poe's (1998, 2004) and Etheridge's (1959) characters. See those papers for more detailed descriptions of skeletal conditions and alternative conditions in *Anolis*.

We scored the new species for the morphological phylogenetic characters of Poe (2004; Appendix 1) and performed a parsimony analysis of these taxa and 251 other species of *Anolis* and eight outgroups with the use of 1,291 parsimony-informative characters from published sources and some of our additional unpublished morphological data. This dataset includes 91 morphological characters (Poe, 2004), 998 sites of mtDNA (NADH dehydrogenase subunit 2, five transfer RNAs; Nicholson *et al.*, 2005), and 182 sites of nuclear DNA (internal transcribed tracer region; Nicholson, 2002). Codes for morphological data for *A. anchicayae* and *A. lyra* are in online Table 1. We used PAUP* version 4.0b10 (Swofford, 2002) to perform a heuristic search with 100 random additions of taxa and tree-bisection-reconnection branch swapping. We also used PAUPrat (Sikes and Lewis, 2001) to perform several runs of the parsimony ratchet (Nixon, 1999) to find optimal

Figure 1. *Anolis anchicayae* new species, male. Photo by Julian Velasco.

trees (20%–35% of characters reweighted, 150–200 replicates per run).

DESCRIPTION OF NEW SPECIES

Anolis anchicayae, new species

Figures 1–5

Holotype. MCZ 160234, adult male, Colombia, Valle, San Isidro, 5 August 1977, Helen Chin.

Paratypes. MCZ 112426–7, Colombia, Chocó, Rio San Juan, Caño Docordo between Cucurrupi and Noanama, 24 December 1968, B. Malkin; MCZ 158385–7, Colombia, Valle, Rio Blanco, road between Cali and Anchicaya (where road crosses river), ca. 500 m along river just above bridge on banana plant, 12 May 1980, H. Carvajal, D. Harris, S. Ayala; MCZ 159767–8, Colombia, Valle, Anchicaya Hydroelectric Central, 3 June 1976, J. Castillo, F. Castro, H. Chin; MCZ 159997–8, 160234–9, Colombia, Valle, San Isidro, Cartón, 5 and 9 August 1977, H. Chin; MCZ 160008–12, Colombia, Valle, Granje Bajo Central, 1976–77, H. Chin, F. Castro; MCZ 160230, Colombia, Valle, Bajo Calima, 14 August 1977, H. Chin; MCZ 160231–3, Colombia, Choco, Bahia Solano, near Jayita, 14–16 October 1977, F. Castro; MCZ 160633, Colombia, Valle, Anchicaya, 7 December 1978, H. Chin, F. Castro; ICN 6115, Colombia, Choco, Bahía Solano, near Jayita, J. Renjifo.

Diagnosis. Anolis anchicayae is similar to *A. peraccae* and *A. fasciatus*. These three species share keeled dorsal head scales, a double row of middorsal caudal scales,

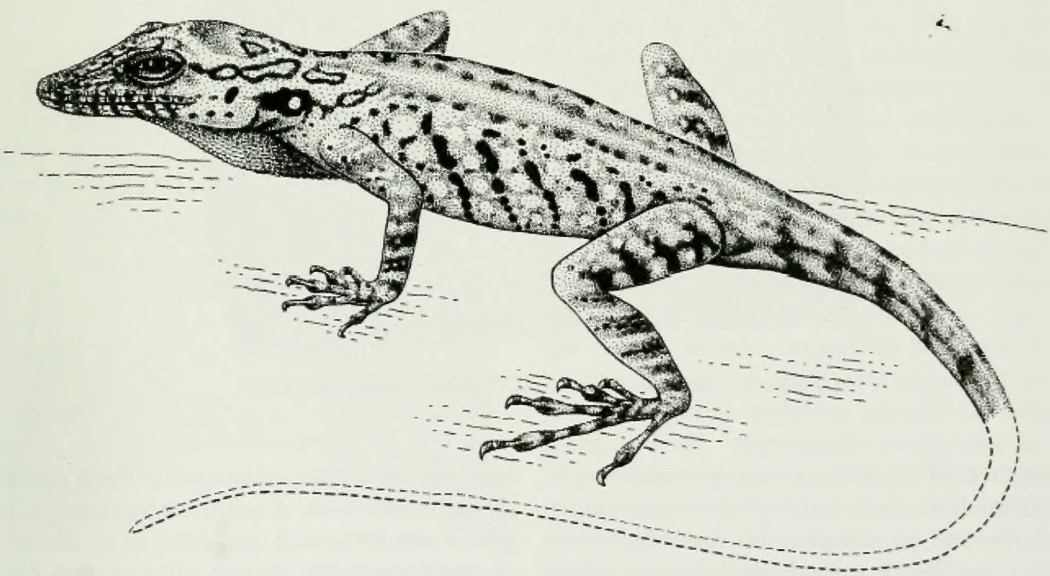

Figure 2. *Anolis anchicayae* new species, MCZ 145362. Tail is missing in this specimen.

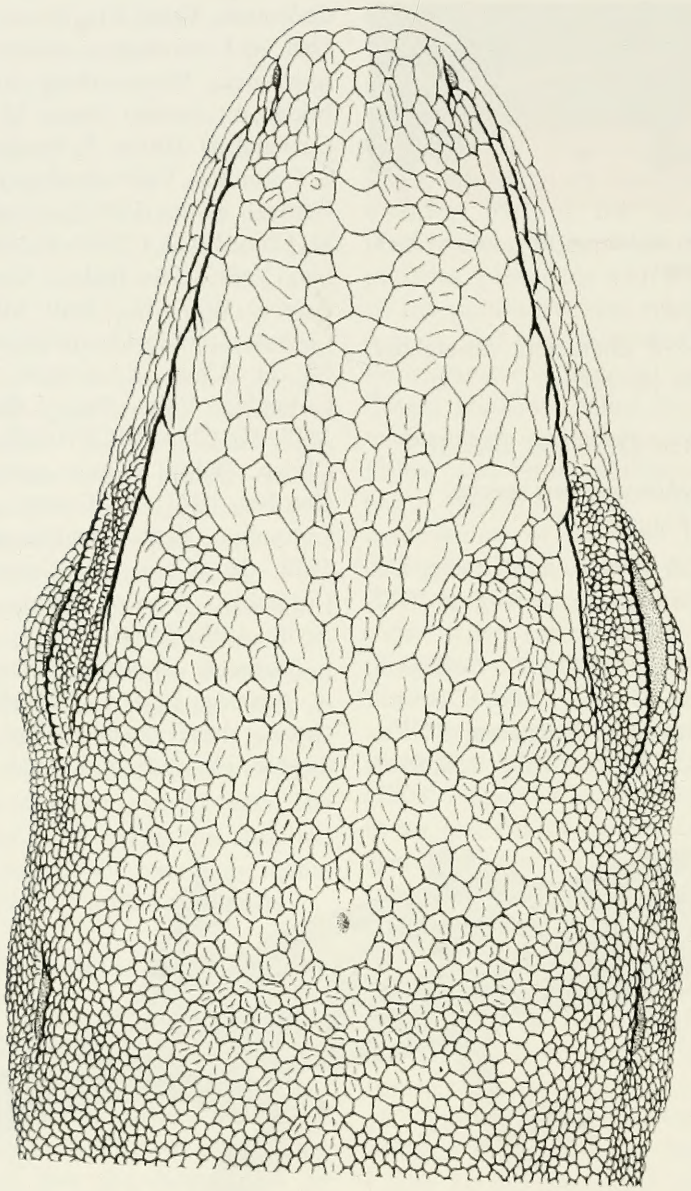

Figure 3. *Anolis anchicayae*, MCZ 145362, dorsal head scales.

absence of dewlap in females, absence of caudal transverse vertebral processes posteriorly, and an elongate anterior nasal scale that reaches the rostral but does not contact the sulcus between the rostral and first supralabial. *Anolis anchicayae* is most easily distinguished from *A. peraccae* by larger size (to 54 mm SVL in *A. peraccae*; to 63 mm in *A. anchicayae*; Fig. 6) and color pattern (*A. anchicayae* is predominantly yellow-green on

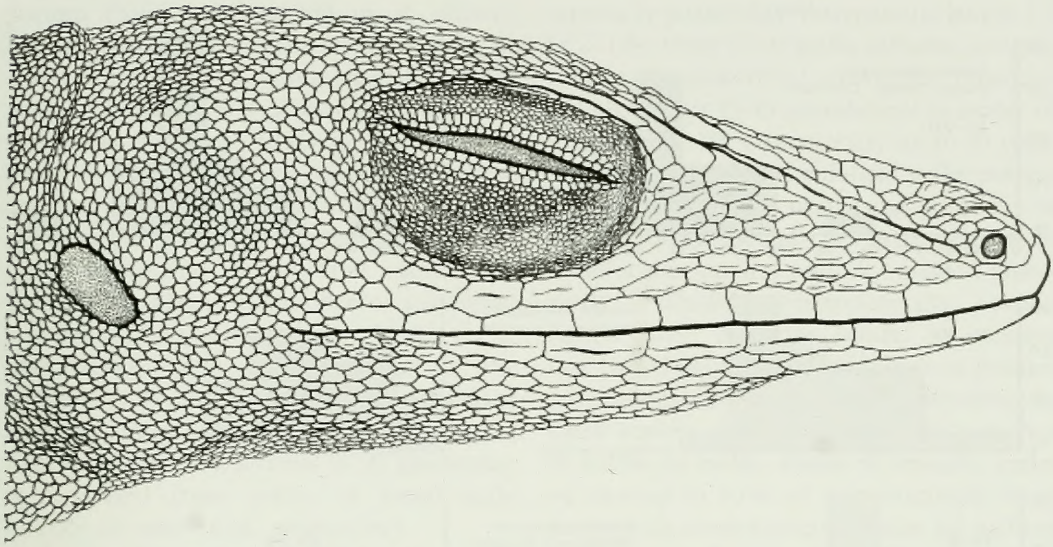

Figure 4. *Anolis anchicayae*, MCZ 145362, lateral head scales.

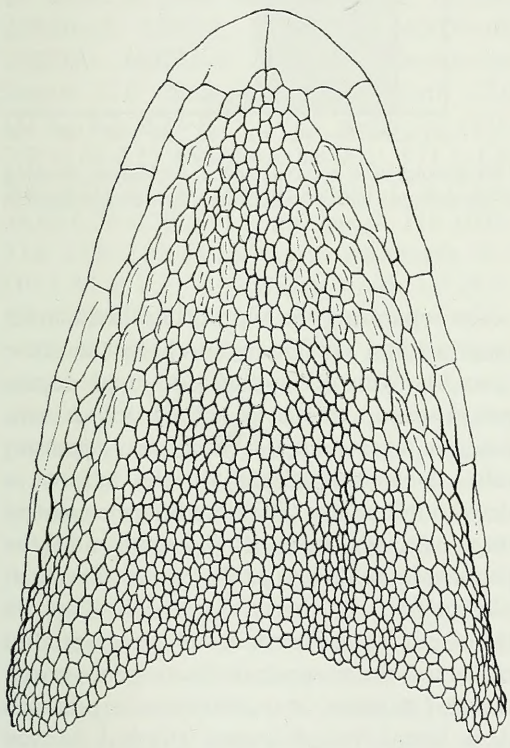

Figure 5. *Anolis anchicayae*, MCZ 145362, ventral head scales.

its flanks with an elongate ocellus from eye to shoulder and a yellow-green dewlap in males; *A. peraccae* is predominantly brown on its flanks with no shoulder ocellus and a cream-colored male dewlap). *Anolis anchicayae* is most easily distinguished from *A. fasciatus* by size (to 72 mm SVL in *A. fasciatus*; to 63 mm in *A. anchicayae*) and male dewlap color (white with gray scales in *A. fasciatus*, yellow-green in *A. anchicayae*).

Anolis anchicayae can be distinguished from other South American *Anolis* as follows (groupings are informal according to Savage and Guyer [1989] and others and used only for organizational purposes; no relationships are implied): from "beta" anoles (= "*Norops*"; with which it is unlikely to be confused) by the absence of transverse processes on posterior caudal vertebrae (present in beta *Anolis*); from phenacosaur and *tigrinus*-group *Anolis* (*A. heterodermus*, *A. inderenae*, *A. nicefori*, *A. bellipeniculus*, *A. carlostoddi*, *A. euskalerriari*, *A. neblininus*, *A. orcesi*, *A. tetarii*, *A. vanzolinii*, *A. ruizi*, *A. solitarius*, *A. menta*, *A. nasofrontalis*, *A. pseudotigrinus*, *A.*

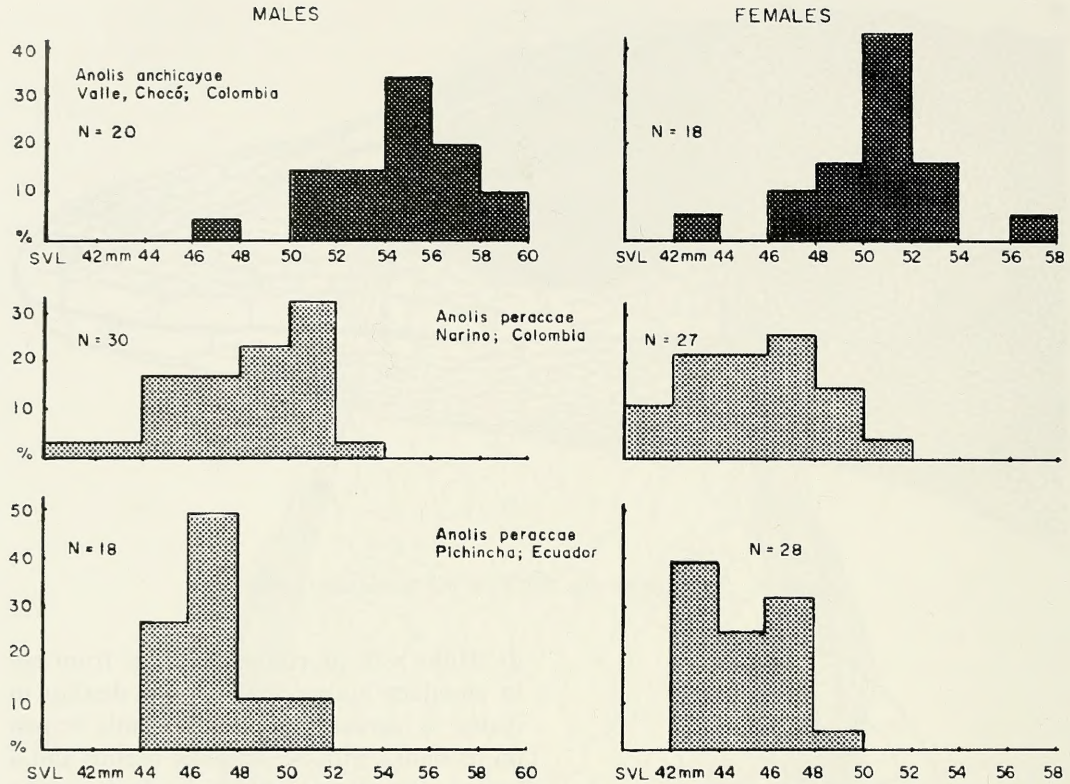

Figure 6. Distribution of body sizes within populations for samples of *A. peraccae* and *A. anchicayae*, showing larger size of *A. anchicayae*. The specimens used to construct this table are unknown because they were not listed in Williams' notes.

tigrinus, *A. menta*, *A. lamari*, *A. vaupesianus*, *A. jacare*, *A. umbrivagus*, *A. paravertebralis*, *A. williamsmitteremeierorum*) by possessing strongly keeled head scales superior to the orbits (mostly smooth or pustulose in phenacosaur and tigrinus-group *Anolis*); from *latifrons*- and some *aequatorialis*-group *Anolis* (*A. latifrons*, *A. frenatus*, *A. fraseri*, *A. danieli*, *A. apollinaris*, *A. casildae*, *A. squamulatus*, *A. princeps*, *A. purpurescens*, *A. agassizi*, *A. eulaemus*, *A. maculigula*) by much smaller size (> 100 mm SVL in these species); from some *punctatus*-group *Anolis* (*A. cuscoensis*, *A. soinii*, *A. huilae*, *A. transversalis*, *A. boettgeri*, *A. deltae*, *A. dissimilis*, *A. santamartae*) by displaying scales separating the supraorbital semicircles (supraorbital semicircles in contact in these species); from other *punctatus*- and *aequatorialis*-group *Anolis* (*A. chocorum*, *A. calimae*, *A. antioquiae*, *A. fitchi*, *A. aequatorialis*, *A. megalopithecus*) in the lack of a dewlap in females (female dewlap present in these species); from *A. punctatus* and the proboscis *Anolis* (*A. proboscis*, *A. laevis*, *A. phyllorhinus*) by the absence of swelling on the snout of the male (swelling present in males of these species); from *mirus*-group *Anolis* (*A. mirus*, *A. parilis*) by the presence of a broad, raised toepad (toepad narrow and continuous with first phalanx in *mirus* group); from *A. chloris* in body color and

pattern (solid bright green in *A. chloris*; banded pattern of browns and greens in *A. anchicayae*); from *A. festae* and *A. nigrolineatus* (the name is a probable synonym of *A. festae*; Williams, 1982) in male dewlap pattern (dark elongate blotch in these species; absent in *A. anchicayae*); from *A. caquetae* in absence of contact between interparietal and supraorbital semicircles; from *A. propinqus* in number of subdigital lamellae (27 in *A. propinqus*, 16–20 in *A. anchicayae*); from *A. gemmosus* in the condition of the nasal scale (elongate anterior nasal contacts sulcus between rostral and first supralabial in *A. gemmosus*; is separated from sulcus by small scale inferior to naris in *A. anchicayae*).

External Description of Holotype (paratype variation in parentheses; description is based on adults in good condition: MCZ 160234, 158386–7, 159767, 159997–8, 160009–10, 160230, 160232–3, 160238). Snout-vent length 52.0 (50.0–53.6); head length 12.0 (11.8–13.2; 0.23–0.25 SVL), width 7.1 (7.0–7.8; 0.14–0.15 SVL); ear height 1.3 (1.1–1.6; 0.02–0.03 SVL); femoral length 12.9 (13.6–16.0; 0.25–0.30 SVL); tail length 115 (102–116; 1.96–2.26 SVL); fourth toe length 10.5 (10.7–11.9; 0.21–0.22 SVL), width 1.0 (1.0–1.3; 0.02 SVL).

Dorsal head scales uni- to multicarinate above orbits, mostly smooth in frontal area, unicarinate on snout; frontal depression present; rostral slightly overlaps mental anteriorly; nine (8–12) scales across snout between second canthals; supraorbital semicircles separated by two (1–2) scales; suboculars in contact with supralabials; one (1–2) elongate supraciliary scale followed by small undifferentiated scales; seven (5–7) loreal rows; elongate anterior nasal scale contacts rostral, is separated from sulcus between rostral and first supralabial by one small scale inferior to naris; supraorbital semicircles evident but not strongly differentiated, especially posteriorly; interparietal length 1.3 (1.2–1.6); three (3–4) scales separate interparietal and supraorbital semicircles; preoccipital absent; six (5–6) supralabials to center of eye; nine (8–10) postrostrals; six (6–9) postmentals; some slightly enlarged scales present in supraocular disc, decreasing gradually in size, bordered medially by a partial row of small scales; mental partially divided posteriorly, extending posterolaterally beyond rostral, with posterior border in concave arc; two (2–4) enlarged sublabials in contact with infralabials (or posteriorly separated by small scales); dewlap reaches well posterior to axillae in males, absent in females; scales on dewlap in rows of approximately three scales with some scattered scales; no axillary pocket; pair of enlarged postcloacal scales in contact (or separated by small scales; absent in females); nuchal and dorsal crests absent; dorsal scales keeled; approximately 10 (5–12) enlarged middorsal rows, six (6–8) longitudinal rows in 5% of SVL; ventral scales in mostly transverse but some diagonal rows, smooth, eight (7–9) scales in 5% of SVL; anterior thigh scales large, keeled, overlapping, becoming smaller and nonoverlapping posteriorly; supradigitals multicarinate; toepads expanded; 19 (16–20) expanded lamellae under third and fourth phalanges of fourth toe (second and third phalanges of Williams [e.g., Williams *et al.*, 1995]); tail with a double row of middorsal scales.

Skeletal Description (Based on Dry Skeletons MCZ 112426–7, 159767, 160012, ICN 6115). Parietal roof flat, with trapezoidal crests, with a very narrow posterior border, with no casquing, lacking crenulation on edges, not extending posteriorly over supraoccipital, with anterolateral corners flush with posterolateral edges of frontal; pineal foramen at parietal-frontal suture (n = 4) or in parietal (n = 1); dorsal skull bones smooth; postfrontal present; prefrontal separated from nasal by anterior extension of

frontal (n = 2) or in contact with nasal (n = 2); frontal sutures anteriorly with nasals; parallel crests on nasals absent; external nares bordered posteriorly by nasals; dorsal aspect of jugal terminates on lateral surface of postorbital; jugal does not contact squamosal; posterodorsal ramus of squamosal shorter than posteroventral ramus, separated from parietal by supratemporal; posterior aspect of jugal mostly straight; epipterygoid contacts parietal dorsally; pterygoid and palatine teeth absent; lateral edge of vomer is smooth, without posteriorly directed lateral processes; maxilla extends posteriorly beyond ectopterygoid on ventral surface of skull (n = 3) or reaches ectopterygoid (n = 2); crest between basipterygoid processes of basisphenoid absent; lateral shelf of quadrate absent; no black pigment on surface of skull; nasals do not overlap premaxilla dorsally; posterior edge of parietal is approximately even with vertical level of parietal-frontal suture; posteriormost mandibular tooth is partially anterior (n = 3 mandibles) or partially posterior (n = 7 mandibles) to anterior mylohyoid foramen; large splenial present; ventral aspect of anteromedial process of coronoid extends posteriorly (n = 4) or slopes anteriorly (n = 1); external opening of surangular foramen is entirely within surangular (n = 1) or bordered by dentary and surangular (n = 3); posterior suture of dentary is pronged; anteriormost aspect of posterior border of dentary is anterior to (n = 3 mandibles) or within (n = 7 mandibles) mandibular fossa; labial process of coronoid present; coronoid does not extend posterolaterally beyond surangular foramen; jaw sculpturing absent; angular absent; angular process of articular present; teeth unicuspid anteriorly, tricuspid posteriorly; nine (n = 3) or 11 (n = 1) premaxillary teeth.

Four postxiphisternal ribs attached dorsally, none free (4:0 rib formula); transverse processes on anterior caudal vertebrae gradually lost posteriorly (Etheridge's [1959] "alpha" condition).

Color in Life (Adapted from Field Notes and Color Photos by Velasco). Males brown middorsally interrupted by approximately 10 dark blotches that extend laterally; flanks greenish-yellow with narrow diagonal rows of partially connected small brown spots; elongate brown mark extending back from eye, bordered by black; upper head part yellow with brown, lateral head brown; ocular border yellow; yellow with brown blotches on lips; dewlap yellow green with brown spots; iris blue; limbs and tail banded. Females with broad middorsal stripe bordered laterally by black; flanks yellow green to yellow with longitudinal very narrow dark brown stripes similar to middorsal stripe.

Distribution. Anolis anchicayae is found throughout the Pacific coastal lowlands of Colombia and Ecuador in primary and secondary humid forest (Fig. 7). Many specimens were collected by day on trunks between 2 and 5 m.

Etymology. The species is named for its type locality, the Anchicaya River valley.

Anolis lyra, new species

Figures 8, 9, 10A

Holotype. MCZ 80955, adult female, Ecuador, Pichincha, Finca Victoria, 37 km SE of Santo Domingo, 16 July 1964, F. Vuilleumier.

Paratypes. MCZ 77458–60, Colombia, Valle, Lower Rio Calima, tributary of Rio San Juan, 1960, I. Cabrera; MCZ 80954, Ecuador, Pichincha, Finca Victoria, 37 km SE of Santo Domingo, 16 July 1964, F. Vuilleumier; MCZ 124407, Ecuador, Pichincha, Santo Domingo de los Colorados, 2 August 1968, J. Lynch; MCZ 145263, Ecuador, Pichincha, Hotel Tinalandia, 15 km N Santo Domingo de los Colorados, 6 November 1964, A. Kiester, E. Williams;

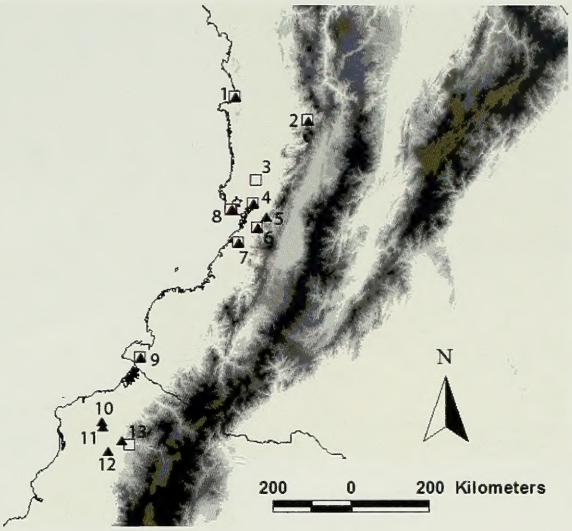

Figure 7. Map of coastal regions of Colombia and Ecuador showing collecting sites of *Anolis anchicayae* (filled triangles) and *Anolis lyra* (open squares) according to type series and personal observations of authors. 1. Nuquí, Chocó Department, Colombia; 2. Pueblo Rico, Risaralda Department, Colombia; 3. Caño Docordo between Cucurrupi and Noanama, San Juan River, Chocó, Colombia; 4. Bajo Calima, Buenaventura, Valle del Cauca Department, Colombia; 5. Cisneros, Buenaventura, Valle del Cauca Department, Colombia; 6. Bajo Anchicaya, Buenaventura, Valle del Cauca Department, Colombia; 7. Cajambre river, Buenaventura, Valle del Cauca Department, Colombia; 8. Málaga Bay, Buenaventura, Valle del Cauca Department, Colombia; 9. Tangareal, Nariño Department, Colombia; 10. Centro Científico Río Palenque, Los Ríos Province, Ecuador; 11. Finca La Victoria, southeast from Santo Domingo de los Colorados, Pichincha Province, Ecuador; 12. Puerto Quito, Pichincha Provice, Ecuador; 13. Hotel Tinalandia, approx. 15 km N of Santo Domingo de los Colorados, Pichincha Province, Ecuador.

MCZ 145867, Ecuador, Los Rios, Centro Cientifico Rio Palenque, 23 June 1974, K. Miyata; MCZ 146994–5, Ecuador, Pinchincha, 1 km N Buena Fe, 31 July 1975, R. Webster; MCZ 152433–4, Ecuador, Pichincha, Hotel Tinalandia, 15 km N Santo Domingo de los Colorados, 27 April 1977, K. Miyata; MCZ 164416, 165209–10, 171160, Ecuador, Pinchincha, Puerto Quito, April and September 1983, December 1984, G. Onore; MCZ 164420–1, Ecuador, Pinchincha, Santo Domingo de los Colorados, April 1983, G. Onore.

Diagnosis. Anolis lyra differs from all other South American *Anolis* except *A. vittigerus* in possessing a small red dewlap with a dark central spot in males and a lyre-shaped symbol in the occipital region (Fig. 8). *Anolis lyra* differs from *A. vittigerus* in possessing smaller middorsal scales (mean number of longitudinal scales in 5% SVL for *A. lyra* = 8.5, *A. vittigerus* = 5.8; $P = 0.006$, Mann-Whitney U test), more scales between supraorbital semicircles (mean = 2.3 in *A. lyra*, 0.6 in *A. vittigerus*; P = 0.001, Mann-Whitney *U* test), and more scales between interparietal and supraorbital semicircles ($\bar{x} = 4.1$ in *A. lyra*, 2.4 in *A. vittigerus*; $P = 0.001$, Mann-Whitney *U* test; Fig. 10). Also, *A. lyra* tends to display much weaker lateral striping (i.e., broken lines only extending to the axillae versus broad stripes to groin in *A. vittigerus*) and a more prominent lyre-shaped posterior head marking (Fig. 8; absent to weak in *A. vittigerus*). In western Colombia, the only area in which both species can be expected to

Figure 8. *Anolis lyra* new species, male, from 2 km N of Boca Ana, Valle, Colombia. Photo by Steven Poe.

Figure 9. *Anolis lyra* new species, female, from 2 km N of Boca Ana, Valle, Colombia. Photo by Steven Poe.

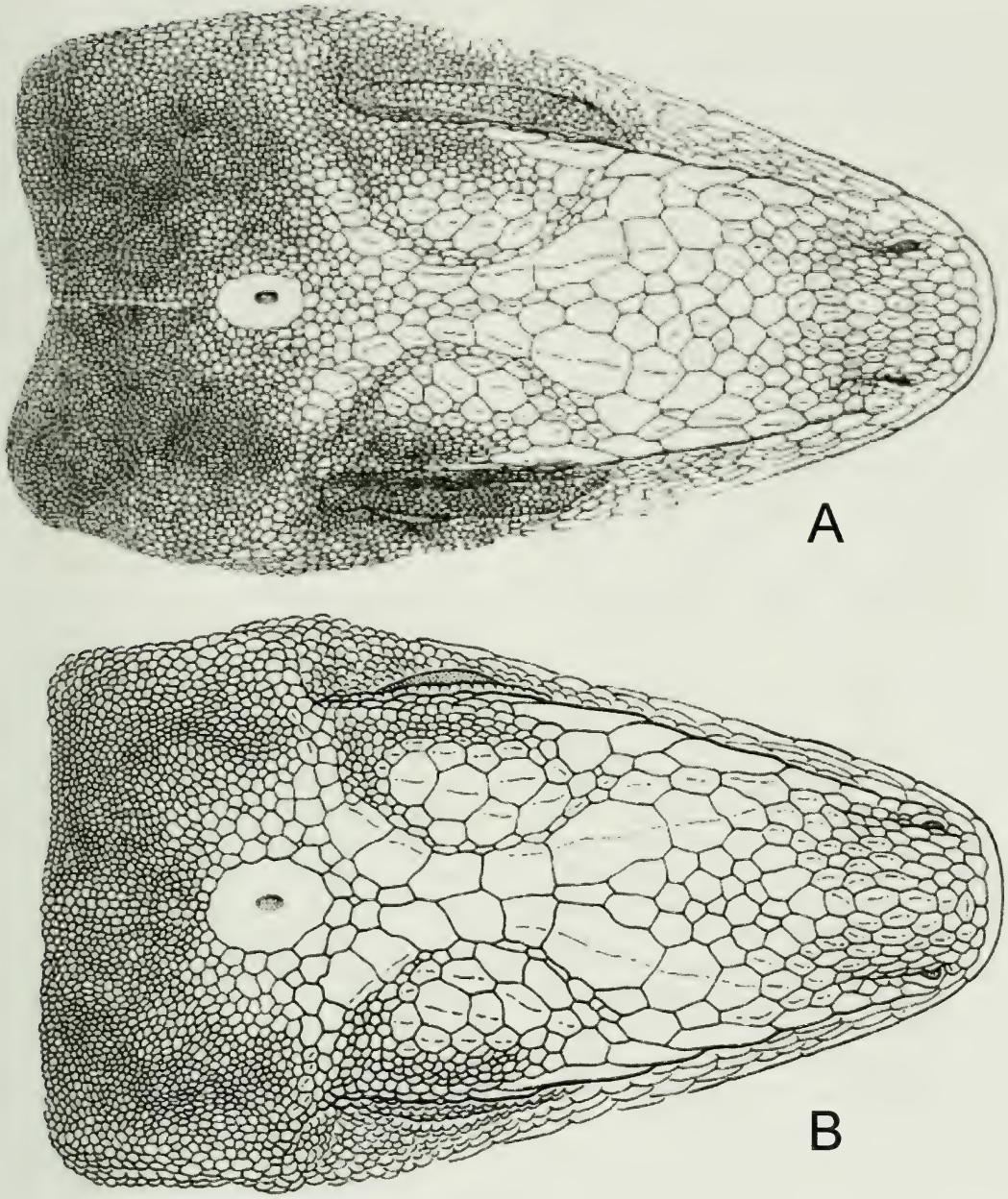

Figure 10. Head scales of (A) *Anolis lyra*, MCZ 77459, Lower Rio Calima, Valle, Colombia, and (B) *Anolis vittigerus*, LACM 42200, upper Rio Napipi, 45 minutes by canoe below mouth of Rio Merendo. These localities are approximately 250 km apart in western Colombia. Note larger scales (e.g., around interparietal) in *A. vittigerus*.

occur, *A. lyra* and *A. vittigerus* may be most easily separated by the condition of the supraorbital semicircles—in broad contact in *A. vittigerus*; usually separated by 2–3 scales in *A. lyra*.

External Description of Holotype (paratype variation in parentheses; description is based on adults in good condition: MCZ 80955, 77458–9, 145267, 145867, 146994–5, 152433–4, 164416, 164420–1). Snout-vent length 76.7 (60.7–75.2); head length 17.8 (14.8–19.6; 0.23–0.26 SVL), width 11.8 (10.1–12.8; 0.16–0.17 SVL); ear height 1.9 (1.2–2.1; 0.02–0.03 SVL); femoral length 22.8 (19.2–24.2; 0.29–0.32 SVL); tail length approximately 165 (128–165; 2.21–2.39 SVL).

Dorsal head scales keeled; frontal depression present; rostral slightly overlaps mental anteriorly; nine (7–11) scales across snout between second canthals; supraorbital semicircles separated by two (1–4) scales; suboculars in contact with supralabials (or separated by one row of scales); two elongate supraciliary scales (or 1–2 slightly elongate scales) followed by parallel rows of slightly enlarged scales; eight (6–10) loreal rows; two scales separate naris and sulcus between rostral and first supralabial; interparietal length 2.0 (1.7–2.3); three (3–5) scales separate interparietal and supraorbital semicircles; preoccipital absent; seven (6–8) supralabials to center of eye; six (6–10) postmentals; eight (6–9) postrostrals; some enlarged scales present in supraocular disc, decreasing gradually in size, bordered medially by a complete (or partial) row of small scales; mental partially divided posteriorly, extending posterolaterally beyond rostral, with transverse (i.e., not concave) posterior border; no (0–1) enlarged sublabials; dewlap just reaches axillae in males, nearly reaches axillae in females; dewlap scales in rows of single scales; weak axillary pocket (not tubelike); enlarged postcloacal scales absent; nuchal and dorsal crests absent; some dorsal scales keeled; zero (0–20) enlarged middorsal rows, 9 (8–9) longitudinal rows in 5% of SVL; ventral scales in diagonal rows, strongly keeled, five (5–7) scales in 5% of SVL; supradigitals multicarinate; toepads expanded; 18 (18–21) expanded lamellae under third and fourth phalanges of fourth toe (second and third phalanges of Williams [e.g., Williams *et al.*, 1995]); fourth toe length 15.6 (14.9–15.6; 0.21–0.23 SVL); scales of anterior thigh large, keeled, overlapping, becoming much smaller posteriorly; tail with a single row of middorsal scales.

Skeletal Description (Based on Dry Skeleton MCZ 77460). Parietal roof flat, with Y-shaped parietal crests, with no casquing, lacking crenulation on edges, with anterolateral corners flush with posterolateral edges of frontal; pineal foramen at parietal-frontal suture; dorsal skull bones smooth; postfrontal present as sliver at rim of orbit; prefrontal separated from nasal by anterior extension of frontal or in contact with nasal; frontal sutures anteriorly with nasals; parallel crests on nasals absent; external nares bordered posteriorly by nasals; dorsal aspect of jugal terminates on lateral surface of postorbital; posterodorsal ramus of squamosal smaller than posteroventral ramus, separated from parietal by supratemporal; posterior aspect of jugal mostly straight; epipterygoid contacts parietal dorsally; pterygoid and palatine teeth absent; lateral edge of vomer is smooth, without posteriorly directed lateral processes; maxilla extends posteriorly beyond ectopterygoid on ventral surface of skull; crest between basipterygoid processes of basisphenoid absent; lateral shelf of quadrate absent; black pigment is present on parietal, prefrontals, and nasals; nasals slightly overlap premaxilla dorsally; posteriormost mandibular tooth is posterior to anterior mylohyoid foramen; splenial apparently absent (difficult to tell); ventral aspect of anteromedial process of coronoid extends

posteriorly; external opening of surangular foramen is entirely within surangular or shares border between dentary and surangular; posterior suture of dentary is blunt, not pronged; anteriormost aspect of posterior border of dentary is within mandibular fossa; labial process of coronoid present; coronoid does not extend posterolaterally beyond surangular foramen; jaw sculpturing absent; angular absent; angular process of articular present, large; teeth unicuspid anteriorly, tricuspid posteriorly; eight premaxillary tooth positions.

Color in Life (Adapted from Field Notes and Color Photos by Poe). Male basically dark brown with pale yellow pattern; middorsum with four light blotches breaking up dark background; butterfly-shaped marking above pelvis; posterior of dorsal head light gray with dark lyre-shaped marking around occipital region (lyre "opens" anteriorly); dark band between orbits dorsally; laterally, a light stripe extends back from area posterior to eye, becoming broken between limbs, bordered ventrally by dark brown; light yellow extends posteriorly from snout along dorsal edge of mouth below dark brown band, broken by dark blotches below orbit; limbs and tail banded with curved yellow lines; dorsal markings less distinct, melding together in some specimens (perhaps in response to stress); venter pale yellow with dark flecks most evident laterally; underside of head pale yellow washed with red, with some dark reticulations anterior to orbits; tongue tan, throat light gray; eyes reddish brown; dewlap skin red with orange tint, with discrete dark central spot; dewlap scales light distally, dark centrally.

Female coloration like male but with bluish-gray dewlap skin with faint red tint and dark central spot.

Distribution. Anolis lyra is found from the Pacific lowlands of central Colombia south to northwestern Ecuador (Fig. 7). Most *A. lyra* were collected sleeping at night in secondary humid forest on twigs or leaves 1–5 m high. Some specimens were collected by day in lower parts of trees and on ground.

Etymology. This species is named for the lyre-shaped marking on the back of its head (Fig. 8).

DISCUSSION

Relationships. Many taxa are scored for as few as 3% of parsimony informative characters (i.e., only external morphological data). Inclusion of such poorly scored taxa will tend to increase the number of most parsimonious trees and thus lower support levels such as bootstrap frequencies (Huelsenbeck, 1991). We nevertheless include these taxa to achieve an estimate of their phylogeny relative to *A. anchicayae* and *A. lyra* and to increase the accuracy of phylogenetic placement of *A. anchicayae* and *A. lyra* (Gauthier *et al.*, 1988; Hendy and Penny, 1989). Because support values are uniformly low and many optimal trees resulted, as expected, we summarize results with a majority-rule consensus of optimal trees.

Results of the phylogenetic analysis of *A. anchicayae* and *A. lyra* are shown in Fig. 11. *Anolis anchicayae* is sister species to *A. peraccae* among an unresolved group of South American alpha *Anolis* (approximately equivalent to Etheridge's [1959] *latifrons* series and Guyer and Savage's [1986] "*Dactyloa*"). The "latifrons" group usually has been found to be monophyletic (including "*Phenacosaurus*"; Etheridge, 1959; Jackman *et al.*, 1999; Poe, 2004, fig. 2; Nicholson *et al.*, 2005) but is occasionally paraphyletic (Poe, 2004, fig. 5; this study) in recent studies. Obviously, more phylogenetic work is needed on the South American alpha *Anolis*.

Anolis lyra is grouped with some other *lemurinus*-group species *A. bicaorum* and *A.*

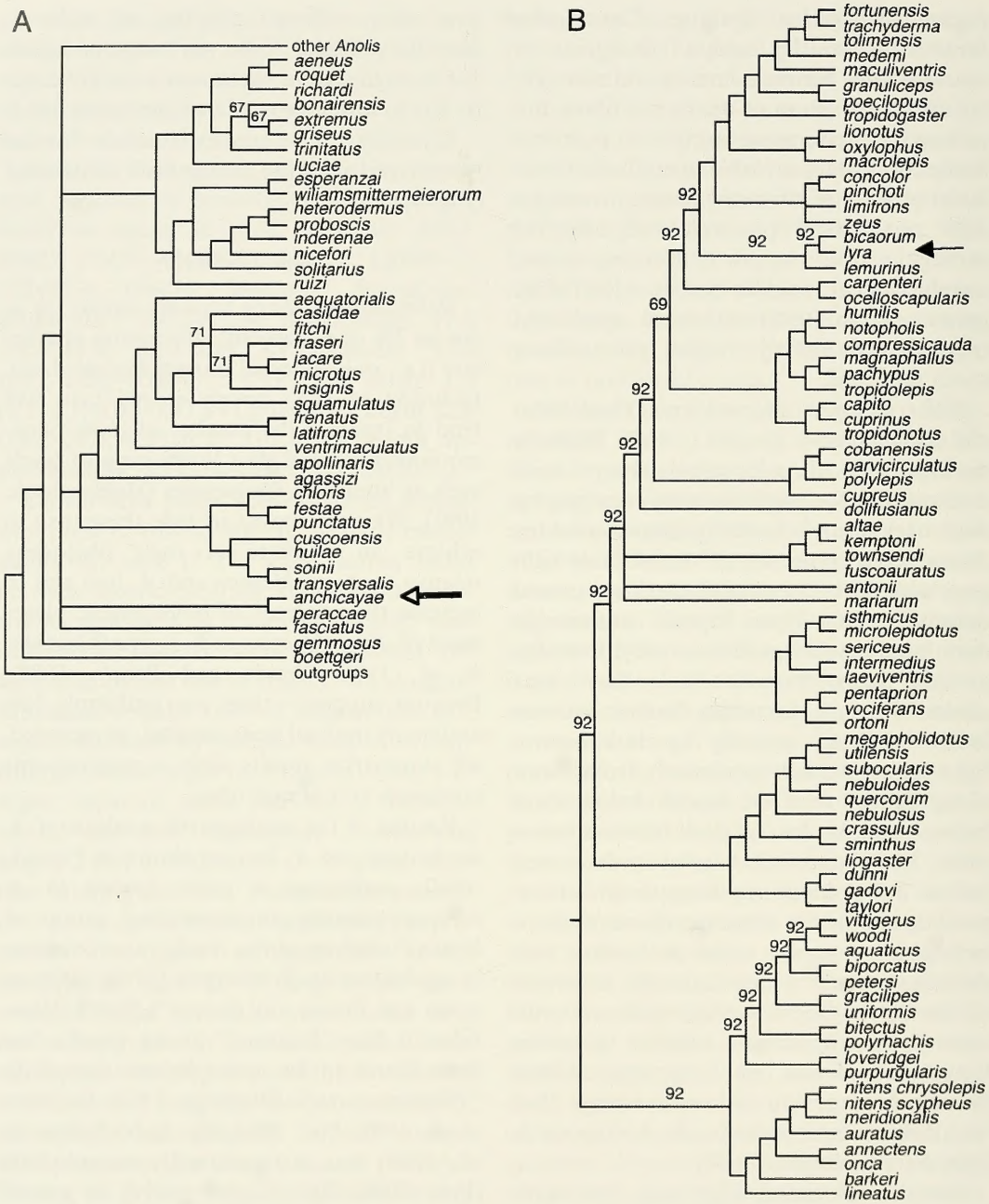

Figure 11. Relationships of (A) *Anolis anchicayae* and (B) *A. lyra* based on parsimony analysis of 1,271 informative characters and 253 species of *Anolis* and eight outgroups. Shown are two portions of the majority-rule consensus of 4,961 maximum parsimony trees (i.e., this is not a bootstrap tree). Relationships present in less than 100% of optimal trees are identified with percentages above those clades or with clade collapsed if present in less than 50% of optimal trees. All taxa are *Anolis*. Figure 9A shows relationships of basal alpha *Anolis* ("latifrons" group sensu lato, "dactyloids"); Fig. 9B shows relationships of mainland beta *Anolis* (mainland "*Norops*"). Other analyzed species are omitted for brevity.

lemurinus within the mainland beta *Anolis* (Etheridge, 1959; = "*Norops*"). *Anolis lyra* shares several *lemurinus*-group characters with these species (e.g., narrow toepads, a dark interorbital bar, lack of enlarged postcloacal scales, dorsal color pattern; see Kohler, 1999). The *lemurinus* group of *Anolis* might be nonmonophyletic (Nicholson, 2002). In the current estimate, this group is composed of three putative clades: *A. lemurinus*, *A. bicaorum*, and *A. lyra*; the large-hemipenes group, *A. tropidolepis*, *A. pachypus*, and *A. magnaphallus*; and *A. vittigerus*. *Anolis vittigerus* is superficially similar to *A. lyra* but displays an unusual combination of characters, including, for example, nasal overlap of the premaxilla. Future studies will examine whether these unusual conditions signal independent evolution or some less interesting phenomenon such as limited sample size.

Remarks. With the description of these two species, the remaining nomen nudum *Anolis* from Ayala (1986) are *A. "jericoensis,"* "*A. malkini,*" and *A. "urraoi."* We have examined specimens of putative *A. "jericoensis"* and are unable to distinguish these from *A. eulaemus*. We are unable to distinguish preserved specimens of putative "*A. malkini*" from *A. pentaprion*. Specimens of putative *A. "urraoi"* are likely to represent a distinct species similar to *A. fuscoauratus* and *A. maculiventris*. *Anolis fuscoauratus* clearly is composed of multiple undescribed species (authors' personal observations); thus, description of *A. "urraoi"* could be challenging.

COMPARATIVE MATERIAL EXAMINED

Museum of Comparative Zoology, Harvard, U.S.A. = MCZ. *Anolis fasciatus* MCZ 143961, 147007, 154126, 151645, 151647. *Anolis peraccae* MCZ 170463, 170465, 170473–5, 170479, 170486–7. *Anolis vittigerus* MCZ 115725, 154549, 158391, 165184, 17190–1. See Poe (2004) for list of additional specimens examined.

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